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Tough decisions: Reproductive timing and output vary with individuals' physiology, behavior and past success in a social opportunistic breeder

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ABSTRACT

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Photoperiod and the hormonal response it triggers are key determinants of reproductive timing in birds. However, other cues and physiological traits may permit flexibility in the timing of breeding and perhaps facilitate adaptation to global change. Opportunistic breeders are excellent models to study the adaptive significance of this flexibility, especially at the individual level. Here, we sought to quantify whether particular male physiological and behavioral traits were linked to reproductive timing and output in wild-derived zebra finches. We repeatedly assessed male stress-induced corticosterone levels (CORT), basal metabolic rate (BMR), and activity before releasing them into outdoor aviaries and quantifying each pair's breeding timing, investment, and output over a seven-month period. Despite unlimited access to food and water, the colony breeding activity occurred in waves, probably due to interpair social stimulations. Pairs adjusted their inter-clutch interval and clutch size to social and temperature cues, respectively, but only after successful breeding attempts, suggesting a facultative response to external cues. When these effects were controlled for statistically or experimentally, breeding intervals were repeatable within individuals across reproductive attempts. In addition, males' first laying date and total offspring production varied with complex interactions between pre-breeding CORT, BMR and activity levels. These results suggest that no one trait is under selection but that, instead, correlational selection acts on hormone levels, metabolism, and behavior. Together our results suggest that studying inter-individual variation in breeding strategy and their multiple physiological and behavioral underpinnings may greatly improve our understanding of the mechanisms underlying the evolution of breeding decisions.

Introduction

It has long been recognized that birds in seasonally predictable environments utilize photoperiod as the main cue to time a suite of physiological changes that brings the individual into a state of reproductive readiness (Nicholls et al., 1988; Dawson et al., 2001). Within this window of physiological readiness, however, there is potential for substantial variability in the onset of breeding itself. For example, recent experimental studies in seasonal breeders revealed that reproductive timing and investment respond to change in temperature whereas the levels of reproductive hormones such as luteinizing hormone (LH) and prolactin were unaffected (Schaper et al., 2012; Caro et al., 2013; Ryan et al., 2014).

Opportunistic breeders are exceptionally well-suited for studying how breeding decisions are modified within windows of physiological responsiveness because they constantly assess whether to start or forego reproduction over prolonged periods of reproductive readiness (Perfito et al., 2007; Hahn et al., 2008). Indeed, these species undergo cycles of gonadal maturation and regression as in seasonal breeders (red crossbill, *Loxia curvirostra*: Hahn, 1995; zebra finch: Bentley et al., 2000; reviewed in Hahn et al., 2008), but show flexible pulses of reproductive activity throughout the year (Wingfield et al., 1992; Hahn et al., 2008). Many Australian bird species, including the very-well studied zebra finch (*Taeniopygia guttata*), breed opportunistically to exploit extremely unpredictable rainfall (Immelmann, 1963; Zann, 1996). While these conspicuous population patterns of boom and bust have been described for a long time in these systems, the triggers of reproduction at the individual level are not understood (Astheimer and Buttemer, 2002).

In contrast, individual differences in the timing of reproduction have been well studied in seasonally breeding birds (Verhulst et al., 1995; Sheldon et al., 2003). In particular, it is well recognized that reproductive decisions are influenced by local weather conditions, individual condition, the stage of the breeding season, and the annual cycle (Wingfield et al., 1983; Verhulst et al., 1995; Dawson et al., 2001; Visser et al., 2009). Within that context of individual differences, the role of physiological traits other than reproductive hormones, such as the activity of the hypothalamic–pituitary–adrenal (HPA) axis, is

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gaining importance. Indeed, a growing number of studies have linked individuals' corticosterone level to variations in reproductive output (Ouyang et al., 2011; Riechert et al., 2014) and timing (Wada et al., 2008; Ouyang et al., 2013). The relationship between these traits varies greatly depending on when corticosterone levels are measured relative to breeding, on the severity of environmental conditions and on whether baseline or stress-induced levels are measured (Wingfield et al., 1983; Ouyang et al., 2011; Riechert et al., 2014; Davies and Deviche, 2014). Stress-induced corticosterone levels may be particularly informative because HPA reactivity is believed to mediate the trade-off between self-maintenance and reproduction at the physiological level (Wingfield et al., 1998). For example in great tits *Parus major*, males' stress-induced corticosterone levels predicted their probability of abandoning their nests when weather conditions severely deteriorated later in the season (Ouyang et al., 2012). Accordingly, stress sensitivity has been linked to both reproductive output and survival in many taxa (reviewed in Breuner et al., 2008).

Glucocorticoids also play a role in the regulation of metabolism and activity (reviewed in Landys et al., 2006). Corticosterone levels may therefore interact with an individual's metabolic and activity levels to shape its breeding decisions in response to specific external cues (Davies and Deviche, 2014). Accordingly, particular individual phenotypes that combine specific levels of stress sensitivity, metabolic rate and activity level might be at a selective advantage. Indeed, there are good reasons to expect that individuals' hormones, metabolism, and behavior may be co-adapted and/or genetically correlated (Réale et al., 2010). Although many studies have demonstrated that natural selection acts on hormonal (McGlothlin et al., 2010), metabolic (Boratyński and Koteja, 2010), and behavioral (Dingemanse et al., 2004) traits, we know very little about the importance of correlational selection among these trait categories. Yet, studies of correlational selection are crucial to understand individual (co)variation from an adaptive perspective (McGlothlin and Ketterson, 2008).

A large body of work has focused on the effect of environmental cues on males' reproductive readiness (reviewed in Dawson et al., 2001). However, the effect of male traits' on the timing of breeding itself has received little attention (compared to females: Davies and Deviche, 2014), with studies on male traits focusing instead on the relative effect on within versus extra-pair young. Males are nonetheless likely to contribute to variation in laying date and clutch size, because of their role in egg fertilization and in some species in territory acquisition, nest building, courtship feeding and incubation (e.g., Auld et al., 2013).

Here, in order to assess whether selection may operate on reproductive timing in an opportunistic breeder and whether some individual phenotypes may initiate population breeding waves, we quantified the relationships between some key physiological traits in male zebra finches and their reproductive investment while in captive colonies. The zebra finch shows some photoperiodic responses in the lab (Bentley et al., 2000) and in the wild (Perfito et al., 2007), although food availability overrides photoperiodic cues (Perfito et al., 2008). In addition, social cues are expected to play a role in breeding phenology (Zann, 1996), which might contribute to the occurrence of waves of breeding activity in wild colonies (Griffith et al., 2008). Pairs may start breeding at any time (Mariette and Griffith, 2012a), but the latency in attempting subsequent clutches increases with the amount of effort put into the previous brood (Mariette et al., 2011). Zebra finches thus face complex allocation decisions both in terms of timing and clutch size in an unpredictable environment.

Over seven months, we monitored the reproductive activity of 61 pairs housed in outdoor aviaries with *ad libitum* access to food and water. First, we investigated the effects of weather, social cues, and past offspring production on population patterns and on individuals' reproductive timing and clutch size. Second, we tested whether reproductive investment varies between individuals but is consistent (repeatable) within individuals and whether timing contributes to total fledgling production. Before breeding, for a subset of "focal" males, we took repeated measures of stress-induced corticosterone levels (CORT), basal metabolic rate (BMR), and activity in both a novel and familiar environments. We then tested whether consistent individual differences in male endocrine, metabolic, and behavioral traits predicted male reproductive timing and clutch size. Finally, we conducted a multivariate selection analysis (Lande and Arnold, 1983) to test whether male reproductive success across the season may be linked to some interactions between hormonal, metabolic, and behavioral traits.

Methods

Study species

The zebra finch is a small, socially monogamous passerine whose distribution encompasses the Australian arid and semi-arid zones, as well as part of the temperate and tropical zones. It is colonial, nomadic, and breeds opportunistically, except perhaps in seasonal climates (Zann, 1996; Perfito et al., 2007). It is very social and cues on conspecifics for nest site selection decisions (Mariette and Griffith, 2012a), with nests typically occurring within two kilometers of standing water (Zann, 1996; Griffith et al., 2008). Social cues are also expected to play a role in zebra finch breeding decisions (Zann, 1996), although this is difficult to verify in the wild. It lays clutches of 2 to 8 eggs (mean 4.9 eggs; Zann, 1996; Griffith et al., 2008) and both parents contribute to nest building, incubation and nestling provisioning (Zann, 1996) and show highly coordinated behavior (Mariette and Griffith, 2012b, 2015).

Experimental subjects

This study was carried out on a colony of wild-derived zebra finches that originated from Northern Victoria in the Australian temperate zone. They had been bred in captivity for approximately 7 to 9 generations and were of mixed age (1 to 5 years old) and with different breeding experiences. Over the spring period prior to breeding, 29 of the 61 males involved in this study had their CORT, metabolic, and behavioral profiles quantified three times, as outlined below (see timeline in Fig. 1). These "focal males" were returned as a single-sex group into an outdoor aviary one month before pairing. The measurements of focal males before breeding had no detrimental effect on their total output (linear model: $t = 0.74$; $P = 0.46$) and first laying date ($t = -1.93$; $P = 0.06$: focal males started slightly earlier) compared to other males. All procedures for maintenance and experimentation were approved by the Animal Ethics Committee of Deakin University (permits G29-2013 and G10-2014).

Design and general procedure of the breeding experiment

Four small outdoor aviaries with single-sex groups were connected to allow birds to pair for 5 days before being captured. At capture, 61 males and 61 females were fitted with a black plastic ring with a unique identity number and two color rings making a unique color combination. Tarsus length was measured using digital calipers (nearest 0.01 mm) and body mass using a digital scale (nearest 0.1 g). All birds were released into a large outdoor aviary ($8 \times 5 \times 2.5$ m) on the 4th December 2013 (c.a. two weeks before summer solstice). Sixty-three nest-boxes were provided the next day, and birds were left to breed freely until early July 2014 (shortly after the winter solstice). Exposure to sun, rain and wind in the aviaries was probably similar to that experienced in thick bushes or trees, since a solid roof only covered half of the area. Three weeks after the start of breeding, the aviary was separated in two equal parts ($4 \times 5 \times 2.5$ m) by an opaque divider, in order to have two sub-colonies within which social cues could be exchanged. Birds were supplied with *ad libitum* seed (Golden Cob finch mix), water, grit and cuttlefish bone; cucumber and water baths were refreshed daily; and cooked whole egg was provided once a week. Nest boxes were checked every morning to record the dates of laying,